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GENETICS

of SUGAR MAPLE



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This publication is one in a series on the genetics of important forest trees of North America published by the Forest Service, U.S. Department of Agriculture, in cooperation with the Society of American Foresters. Development of this series is in accord with the resolutions of the World Consultation on Forest Genetics and Tree Improvement at Stockholm in 1963 and by the Fifth World Forestry Congress in Seattle, 1960. The Committee on Forest Tree Improvement of the Society of American Foresters undertook the preparation of manuscripts for North American species.

Genetics of Sugar Maple

by

H. B. Kriebel and W. J. Gabriel¹

INTRODUCTION

Research on the genetics of sugar maple (*Acer saccharum* Marsh.) has yielded much information on taxonomy and biosystematics, genecology, and reproductive biology. Comparatively little is known about the degree or mode of inheritance of



Figure 1.—This is a typical, open-grown sugar maple showing the dense crown, good diameter growth.

important characters; most of the few existing progeny tests deal mainly with the inheritance of sap sugar content.

Results of taxonomic and biosystematic investigations are important to the geneticist because of the dynamic nature of evolution within the species. Particularly valuable was a series of studies based on population sampling. This work provided a base for variation studies by forest geneticists from 1953 to 1968. More supporting knowledge resulted from the study of natural variability in the sugar content of maple sap in indigenous forest stands. This work, conducted independently in several States during the late 1940's and early 1950's, made possible a program of selection and breeding for high sap sugar content. More information needed for breeding was provided by research on the biology of sexual reproduction, including crossability studies.

The extensive research undertaken to develop an efficient method for vegetative propagation has been less productive because of lack of knowledge of the related fundamental biological processes. There is also little information on the physiology of juvenility. This information is needed because of the long reproductive cycle of the species, with the consequent difficulty of conducting a long-range breeding program.

Taxonomy

Sugar maple has long been recognized as a genetically variable tree, and has received much attention from taxonomists. Besides the typical sugar maple, there are several geographic types which have been listed as individual species by some authors (Pax 1902, Rehder 1949, Fernald 1950, Little 1953), whereas others have considered them to be varieties or subspecies (Britton 1889, Sargent 1891, Desmarais 1952).

Studies of the variation between these taxa have been based mainly on leaf characters because bark

¹Respectively Associate Chairman, Department of Forestry, Ohio Agr. Res. and Develop. Center, Wooster, Ohio, and Geneticist, Northeastern Forest Exp. Sta., USDA Forest Serv., Burlington, Vt.

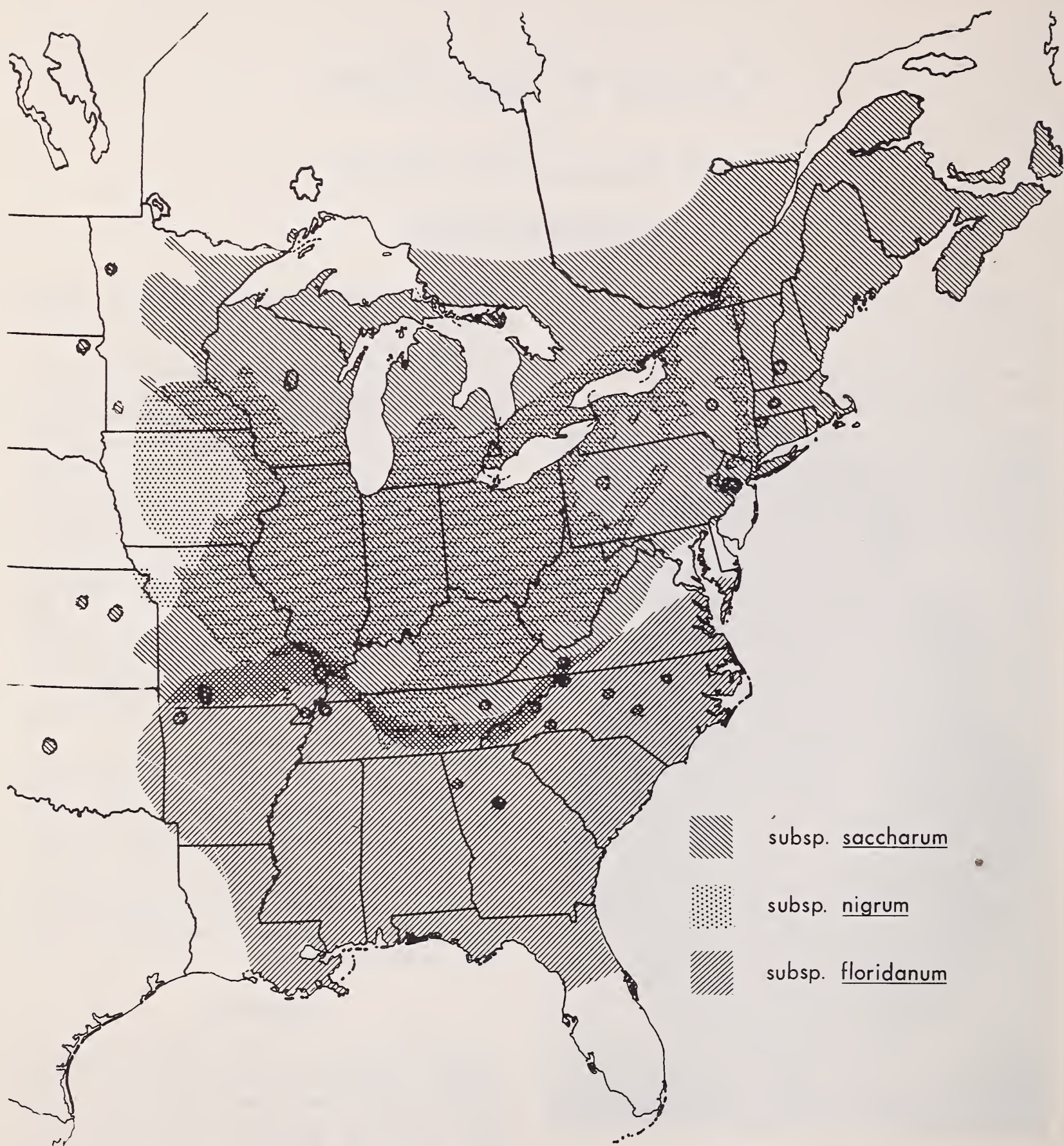


Figure 2.—Distribution of *Acer saccharum* Marshall in Eastern North America (Desmarais 1952, Kriebel 1956, Flaccus 1965, Fowells 1965).

and twig characters have not been reliable criteria for differentiation. They include the work of Beal (1894), Anderson and Hubricht (1938), Dansereau and Lafond (1941), Dansereau and Desmarais (1947), and Desmarais (1952).

The results of this extensive research showed that there was a "flow of characteristics" linking the taxa in a population best defined as a species, *Acer saccharum* Marshall. The elements of the species had wide geographic distribution and were divisible into minor geographic taxa; therefore, they were recognized as subspecies (Desmarais 1952). These results were supported by data from the analysis of a large number of young trees in the nursery stage of provenance tests (Kriebel 1957a). There is no comparable body of experimental evidence to support the thesis that the sugar maples should be recognized as distinct species.

Desmarais described six subspecies in detail. Three occupy extensive geographical regions; in their pure form they have distinctly different leaf characteristics (fig. 3). Of the three, subspecies *saccharum* (sugar maple) and *nigrum* (black maple) are sympatric over a large geographical region, whereas subspecies *floridanum* (Florida or southern sugar maple) is largely allopatric.

Two of the other three forms of sugar maple are of minor importance. One, Desmarais' "subspecies *leucoderme*," is intermediate in leaf outline between *floridanum* and *nigrum*. It also hybridizes with *saccharum* (Slavin 1954). *Leucoderme* is restricted to a few valleys in the southern Appalachians and the Piedmont. Another minor element is "subspecies *Schneckii*." According to Desmarais, it is intermediate in leaf characters between *saccharum*, *floridanum*, and *grandidentatum*. It occurs in the zone where the ranges of *saccharum* and *floridanum* meet (fig. 2).

The sixth element is subspecies *grandidentatum*, a small tree with leaves somewhat resembling those of *floridanum*. *Grandidentatum* forms isolated colonies in deep canyons in western region from Missouri and Arkansas to Idaho, Arizona and northern Mexico. Near its eastern range limits, it intergrades with *floridanum*.

The name *Acer barbatum*, used by Fernald (1945) to designate the subspecies *floridanum*, is incorrect. Although historically preceding *Acer floridanum*, it is based on a type specimen made of several different plants, of which only the flowers belong to any member of the sugar maple complex. The bearded calyx, the probable source of the name *barbatum*, is not restricted to subspecies *floridanum* (Desmarais 1952).

There is clinal variation in leaf characters between *saccharum* and *nigrum* in several geo-

graphic regions (Dansereau and Desmarais 1947, Reimer 1951, Desmarais 1952). Frequency curves of Quebec populations show two distinct summits, implying an active process of hybridization (Dansereau and Desmarais 1947). The trend is toward assimilation of *nigrum* into *saccharum* (Dansereau and Desmarais 1947, Reimer 1951).

Though taxonomy of the sugar maples is based almost entirely on leaf characters, there are other differences among the three principal subspecies. In Ohio provenance tests, subspecies *floridanum* has forked repeatedly and become very bushy.



Figure 3.—Leaf outlines of the major taxa of sugar maple in eastern North America. Top, subsp. *saccharum*; center, subsp. *nigrum*; bottom, subsp. *floridanum*.

While it may have fewer branches in its native habitat than it does in Ohio, it lacks the straight stem characteristic of forest-grown *saccharum* and *nigrum* in the north. It is smaller than either of these other subspecies. Its fruits, small compared with those of northern taxa, and its mainly allopatric distribution indicate that *floridanum* may be nearly at the evolutionary level of a species.

Differences between *saccharum* and *nigrum* are not nearly as pronounced as are differences between these northern elements and *floridanum*. Both of these hard maples are large trees, similar in size, habit and bark characteristics; however, they differ slightly in site requirements. *Nigrum* is frequently found on lower, moister, and slightly cooler areas in regions where it is associated with *saccharum* (Deam 1940, Reimer 1951).

Phylogeny

A. saccharum Marsh. probably existed as a species prior to Pleistocene glacial periods (Braun 1950, Stebbins 1950). If it did, any effect of cold period migrations on genetic differentiation has been within an already existing species. Evidence of migration in glacial and postglacial times is very sketchy. According to one hypothesis, the species moved northward by two routes with the retreat of glaciation. The first movement was along the Appalachians. Movement northward across

Ohio and Indiana was delayed by a warm post-glacial period. As a result, the beech-maple forests of the northern Lake States were derived from westward expansion after the northern migration, and not from migrations from the south (Braun 1950).

The other theory is that there may have been migration with equal rapidity to the west and north from a southern Appalachian refugium, with subsequent elimination of the *saccharum* type from the central western part of the region, leaving *nigrum*. According to this theory, with the return of a cooler and more humid climate, *saccharum* is expanding its range (Desmarais 1952). Apparently, *nigrum* is better adapted to prairie regions, and it is the only hard maple now found in central and western Iowa (Aikman and Smelser 1938). This apparent adaptive superiority in prairie regions is difficult to understand, in view of the previously mentioned observations that *nigrum* occupies a slightly more mesophytic site than *saccharum* in regions farther east.

The *floridanum* element is the only hard maple now found in the Gulf and Atlantic Coastal Plains. It also extends into the Piedmont. The ecology of *floridanum* indicates that it may be a relic from past migrations, occurring in scattered localities where northern plant species persist (Braun 1950).

SEXUAL REPRODUCTION

Flowering Characteristics

The flowers of *A. saccharum* Marsh. are pseudo-hermaphroditic; although both sexes may be present in one flower, only one sex is functional (Gabriel 1968). Pistils in the male flowers are rudimentary and are generally difficult to find. Anthers in the functionally female flowers do not dehisce, though they appear normal except for shortened filaments. No differences have been found between pollen grains from functional and nonfunctional anthers (Gershoy and Gabriel 1961).

The flowering habit of the species is primarily monoecious. There are, nevertheless, definite tendencies toward dioeciousness. The authors have seen trees that were predominantly male or female in blooming characteristics in the northeastern and central parts of the species range. This characteristic is transmitted through grafting. In eastern Pennsylvania, Wright (1953b) noted some trees which produce only male flowers and fewer trees producing only female flowers.

The distribution of flowers may be quite erratic. In some trees, flowers of both sexes may be produced in the upper part of the crown, but only male flowers in the lower part (Gabriel 1962a). Wright (1953b) observed that certain major limbs of trees bore male flowers, while others produced female flowers. Localization of flowering seems to be most obvious during years in which flowering is extremely light. Instead of being sparsely distributed over the entire crown, all flowers may be concentrated on one limb.

Dichogamy seems well established in the species. Gabriel (1968) found that protogyny and protandry were equally prevalent in northern Vermont. Normal and below-normal temperatures during the blooming of protogynous trees favored the expression of incomplete dichogamy, whereas above-normal temperatures tended to favor complete dichogamy. Temperature appeared to have little effect in protandrously-blooming trees. Kriebel observed that dichogamy was incomplete in northern Ohio, and that more trees were

protogynous than protandrous in blooming habit. Dichogamy is also incomplete in southeastern Pennsylvania (Wright 1953b).

Flower Development

Flowers occur in mixed buds; the rachis of the inflorescence is an extension of the tip of the vegetative shoot. The latter consists of two pairs of leaves and a short, relatively thick stem. In the bud, the leaves are arranged upright about the inflorescence. Before physiological activity accelerates in the spring, it is difficult to distinguish between mixed and vegetative buds on the basis of external characters. During prolonged periods of warm weather, mixed buds swell quickly and become four-sided. The rapid radial enlargement of the bud relative to its length causes a change in apex shape from acute to obtuse. This transition is accompanied by a change in color from dark brown to brownish tan. Vegetative buds enlarge much more slowly than mixed buds and maintain their dormant appearance longer. Following bud-break, the inflorescence develops more rapidly than the shoot. In protandrously blooming trees, the anthesis of male flowers occurs before the leaves become prominent.

Gabriel (1966) found that the receptive stage of flowers began about 22 hours after bud-break under greenhouse conditions. The height of the receptive period was reached 38 hours after bud-break; by the 95th hour, decline was evident. Male flower anthesis began 63 to 72 hours after bud-break.

Floral Structure

The arrangement of flowers on the floral axis does not seem to fit any of the definitions used in the classification of inflorescences. According to its structure, the inflorescence of *A. saccharum* Marsh. appears to be in a transitional stage between a *thyse* and a *corymb*. Branching varies progressively from *opposite* and *decussate* in the lower region of the floral axis to *alternate* in the upper portion (Gabriel 1968).

Female flowers are borne in buds that are primarily terminal. Lateral buds are nearly all male, except in extremely rare instances when a single female flower may be observed in an inflorescence.

There is an apparent correlation in flowering plants between the requirement of pollination by bees and the role of floral characters in the differentiation of species. Forty percent of the taxonomic characters used in classifying bee-pollinated plants into species pertain to flowers, though in

wind-pollinated plants floral characters represent only 4 percent of the taxonomic criteria (Grant 1949). The maples, primarily bee-pollinated, are a good example; floral characters are important criteria for species differentiation (Wright 1953a).

Based on a study of floral anatomy, Hall (1951) arranged nine species in the genus into a single phylogenetic series. *A. saccharum* Marsh., because of its lack of petals and their vascular supply, and because of its closed sepal gaps, was ranked midway in the group.

Periodicity and Sexual Maturity

Periodicity of flower crops has been observed in different parts of the species range. Nearly complete failure of flowering was noted in parts of Vermont and Massachusetts in 1957, 1961, and 1965, but in some intervening years flowering was very heavy. Wright (1953b) found that flowering was not constant in the area around Philadelphia, Pa. Among 47 trees observed, about half produced no female flowers during a 4-year period, two trees produced female flowers in 3 of the 4 years, and the remainder produced female flowers in 2 of the 4 years. Kriebel noted that in north-central Ohio heavy crops of female flowers were produced every year by certain trees with a relatively high sap sugar content. Eyre and Zillgit (1953) reported that good seed crops occur at 3- to 7-year intervals in the Lake States, and that light crops are produced in other years.

Under natural forest conditions, light seed crops have been observed on 40- to 60-year-old trees with 8-inch diameters. Moderate crops were noted among 10-14-inch trees 70-100 years old (Fowells 1965).

In Ohio, ramets derived from some trees of flowering age began to produce flowers 7 years after grafting. Moderate to heavy flowering occurred 9 years after grafting. Graft age at first flowering, relative fruitfulness and sex expression were related to clonal line.

Compatibility and Crossability

Inbreeding experiments conducted in Vermont and Massachusetts have shown that there are significant differences between trees in self-fertility (Gabriel 1962a). Seed set in terms of flowers pollinated ranged from 8 to 27 percent. Seedlings from self-pollination varied from small, stunted individuals with small leaves to exceptionally tall, vigorous plants.

Natural selfing probably occurs in sugar maple. Differences in blooming time between male and

female flowers strongly favor cross-pollination, but sufficient overlap occurs for a limited amount of selfing to take place (Wright 1953b and personal communication).

Cross-compatibility studies have shown that variation in seed set after cross-pollination cannot be consistently related to the general performance of either the male or the female parent. The close relation of seed set after cross- and self-pollinations of a given female parent indicated that self- and cross-sterility were associated. The expression of agamocarpy is quite strong in the species; fruit sets ranging from 36 to 94 percent were noted among unpollinated flowers of individual trees. In a study of agamospermy, less than 1 percent of the unpollinated flowers produced filled fruits (Gabriel 1967).

Crossability studies have demonstrated that a genetic barrier exists between *A. saccharum* Marsh., the only species in its section, and all other sections of the genus. Only one partial exception has been reported. This was a cross of *A. platanoides* x *saccharum*, yielding a few poorly filled seeds that did not germinate (Wright 1962).

Controlled Pollination

Since the species is insect-pollinated, porous or loosely-woven bags can be used for controlled pollination. White cotton bags or white parchment paper bags are suitable. Flowers in dark-colored cloth or paper bags are killed by overheating.

Bags should be applied before female flower anthesis, and should be removed soon after the receptive stage is passed. Male and female flowers are borne in the same clusters but open at different times; dissection of a few unopened flowers of a particular size on each branch is necessary to determine the average condition of the branch. Emasculation may be necessary and is easily accomplished by removing the male flowers with the fingernail (Wright 1962).

In *A. saccharum* Marsh., 15 to 20 four- to five-flowered buds or 2 to 3 eight- to ten-flowered buds can be included in each bag. Pollen can be forced in the greenhouse on grafted branches, but only with difficulty on cut branches in water. Pollen is best applied by using freshly opened anthers as pollinating brushes. It can also be applied from a vial with a camel's hair brush.

For practical reasons, it is necessary to limit pollination to the lower branches of open-grown trees. Reasons are: (1) The greater efficiency of working on the lower branches from a short ladder; (2) the equal distribution of female flowers

over the outer portion of the sunlit crown; and (3) the need to dissect and examine unopened buds when bagging (Wright 1962).

Seed sets have been obtained from crosses with pollen stored for 16 days, but the maximum storage life has not been determined (Wright 1953a).

Nursery and Field Practice

Seeds have been successfully stored for 41½ years at moisture contents of 10 and 17 percent at 7° to 10° C. (Yawney 1968). Empty and filled samaras can be separated, prior to storage or planting, by floating in pentane (Carl and Yawney 1968).

Seed sown in the spring must be pretreated by stratification in a medium such as moist sand or peat for 60 to 100 days, depending on seed origin, at about 4° C. Carl and Yawney (1964) obtained consistently good results when they stratified seed in perlite, sand, sphagnum moss, or germination paper. Stratification must be timed to prevent premature seed germination.

Tests of fall sowing versus spring sowing of seeds in New York and Vermont showed that germination was highest after fall sowing (Heit 1935; Yawney 1968).

A sowing density of 15 seedlings/ft² (160/m²) is desirable, although this figure may vary, depending on nursery growing conditions and the length of time that the seedlings are to remain in the seedbed (Stoeckeler and Jones 1957). Logan (1965) found that seedlings grew taller under conditions of full sunlight than when grown under 55 to 87 percent shade, but Stoeckeler and Jones (1957) reported that sugar maple seedlings grew best under 50 percent shade.

Nursery fertility criteria for the species were developed by Wilde and Patzer (1940), based on an analysis of forest soils supporting undisturbed natural stands of sugar maple. Seedbeds may require protection from rodents as well as insects. MacCollum and Yawney (1967) reported heavy seed losses in the nursery, caused by the larva of the fly *Hylemya florilega* (Zetterstedt).

Mulching between rows of sugar maple transplants with a combination of black polyethylene film and sawdust can effectively control weeds and promote good growth (Gabriel 1962b). Satisfactory control of weeds and insects in seedbeds has been obtained for 1 year by use of a commercial soil fumigant composed of 98 percent methyl bromide and 2 percent chloropicrin.

Experimental plantations of sugar maple designed for genetic studies or seed orchards should be established on good planting sites. Wallihan

(1949) has pointed out that failures of sugar maple plantations in New York resulted from poor sites, vegetative competition, frosts, and animal damage. Research will be needed before sugar maple plantings can be successfully established on eroded sites. Techniques used successfully in Ohio in the establishment of experimental plantings include the use of agricultural land, cultivation before planting and for 2 years thereafter, fall hand planting of 3- or 4-year-old stock, mulching with sawdust,

and annual fertilization for several years, beginning 1 year after planting.

In Vermont, field tests of sugar maple were successfully established by liming, fertilizing, and plowing of old fields, hand planting stock that was a minimum of 15 inches in height, and mulching the trees with 30-inch squares of 4-mil black plastic. Control of competing vegetation by the use of herbicides is now becoming a standard practice in hardwood plantations.

ASEXUAL REPRODUCTION

Budding and Grafting

Budding is used almost exclusively by commercial nurserymen for the vegetative propagation of sugar maples. Up to 95-percent success may be obtained. Budding of northern genotypes must be done in early summer, or the bark will not slip.

Grafting of scions is more time-consuming than budding and less successful in field operations. It has been very useful, however, for greenhouse propagation of selected biotypes in research and seed orchard development. A multifactor experiment by Kriebel showed that scion vigor was the most critical factor in survival of grafted scions in the greenhouse. A much higher percentage of successful grafts was obtained from vigorous than from slow-growing trees. Geographic source of scions, type of graft, composition of potting mixture, type of humidity enclosure, date the stocks were brought into the greenhouse, and location in the greenhouse were less important factors affecting survival.

Rooting of Cuttings

Efforts by earlier workers showed that cuttings taken from mature sugar maples generally rooted with difficulty. Afanasiev (1939) reported negative results in his study of the effects of various concentrations of indolebutyric acid (IBA) on the rooting of greenwood cuttings.

Snow (1941) was unable to root cuttings taken from mature trees, but he found that greenwood cuttings from 4- to 5-year-old saplings rooted quite readily. Increased rooting was noted among cuttings taken from 5-year-old saplings when the cut ends were soaked for 3 hours in a 5-percent concentration of IBA. Similarly, Enright (1958) was successful in rooting sugar maple cuttings when the basal ends were dipped in a 10- to 20mg./ml.

IBA solution. He also noted that cuttings collected in June gave a higher rooting percentage than those collected in other months.

Doran (1957) found that 57 percent of the cuttings taken in early June rooted when treated with IBA in powder form at a rate of 1 mg./g. The percentage was lower after treatment at concentrations of 3 mg./g. or 8 mg./g. He obtained rooting of 46 percent of cuttings dipped into a 0.25 percent IBA solution. Untreated cuttings did not root. The rooted cuttings failed to survive the winter in either a greenhouse or a cold frame.

Dunn and Townsend (1954) investigated the effect of 10 growth regulators on rooting of sugar maple cuttings taken from mature trees. The best rooting was obtained when cut ends were dipped into a 1-percent IBA solution. A marked and consistent clonal difference in rooting was observed among the ortets used in the experiment.

In further studies of the effects of growth regulators on rooting, Dunn and Eggert (1959) observed no significant differences between treated and untreated cuttings. Strong clonal differences in rooting ability were found to be constant from year to year. The investigators reported the first successful overwintering of rooted cuttings, but they were unable to duplicate the results in the following years.

Significant differences in rooting among clones and among rooting media were found by Gabriel, Marvin, and Taylor (1961). Working with cuttings from 46 mature sugar maples, they obtained more than 1,000 rooted cuttings. These were stored for the winter in a root cellar with a temperature range of 1° to 4° C. and a relative humidity above 80 percent. None of the cuttings survived, although a few instances of bud-break were observed in the following spring. Repetition of the experiment in the following year indicated a lack of consistency among clones in rooting ability. This implied that

the physiological condition of the cuttings at the time of collection may be an important factor in their rooting capacity.

Air Layering

The method of vegetative propagation that has received least attention from research workers is air layering. According to Fayle (1964), natural layering of sugar maple is more common than is generally realized. Seedlings, branches, stems and basal sprouts may become layered.

Sugar maple will also layer under artificial conditions. Fröhlich (1957) obtained 100-percent success in air layering of 5-year-old trees by girdling

branches and then applying a 1-percent concentration of the potassium salt of IAA or IBA in powder form to the girdled areas. Moist sphagnum moss and polyethylene film were wrapped around the girdle. Root formation was observed within 4 to 5 weeks after treatment.

Cunningham and Peterson (1965) reported a successful technique for air layering mature sugar maples. Girdled areas of different widths, at both nodes and internodes of branches, were treated with 0.8 percent IBA in talc. Among 10 ortets used in the experiment, rooting varied from 10 to 100 percent, averaging 67 percent. Branches girdled at internodes failed to root. The optimum width of the girdle was 2.5 cm.

GENETICS AND BREEDING

Variation in Winter Hardiness

In view of its extensive latitudinal range, the variation in winter hardiness of hard maple cannot be considered pronounced. In Ohio, in provenance tests now 15 years old, the only noticeable dieback from winter or frost injury has occurred in trees of the *floridanum* subspecies from Georgia, western Florida, and southern Mississippi. These trees stop growing very late in northern localities. There is some variation in winter hardiness among the southern trees. Most Florida trees are severely injured, but some Georgia trees are barely affected. Trees of southern Illinois origin are related to *floridanum* trees, but they can endure -28°C . without injury. These relict populations in the Deep South and Mississippi Valley apparently retain a genetic capacity for winter hardiness usually found only in trees of northern genotypes. The contrast with observations on southern collections of some species of *Fraxinus* and *Quercus* is quite pronounced (Wright 1944a, 1944b, Gabriel 1958, Kriebel 1959).

Frost injury to shoots of early flushing trees of northern origin was observed in the nursery (Kriebel 1957a), but it has had a very minor effect, if any, on older trees planted in the field.

Variation in Tolerance to Summer Heat and Drought

The pattern of variation in heat and drought resistance is related to the regional pattern of mean and maximum summer temperature. Includ-

ing *floridanum*, the response pattern forms three recognizable ecotypes. One consists of subspecies *floridanum*; it is characterized by a minimum of seedling mortality resulting from drought and very little seedling leaf scorch under high insolation. Another ecotype includes trees of both *saccharum* and *nigrum* elements originating in the comparatively cool and humid hemlock-white pine-northern hardwood region, including the Appalachians, the Northeast, the northern portions of the Lake States, and the entire distribution of the species in Canada. These trees are most susceptible to leaf injury and drought. A third ecotype includes *saccharum* and *nigrum* trees from the remaining central and western part of the species range, which suffer moderately from leaf scorch and are highly resistant to drought.

These ecotypes are only as distinct as the summer climates of their three geographic regions. There is variation within each ecotype and there are probably zones of intergradation. There is also evidence of an east-to-west clinal gradient of increasing drought resistance in the central hardwood group of population samples. Words are inadequate to describe such intraspecific variation, but a pattern of comparative regional uniformity does exist in this species which appears to justify reference to three ecotypes varying in response to summer environment (Kriebel 1957a). The geographic distributions of these ecotypes should not be confused with those of the subspecies (fig. 2). The latter are based solely on leaf morphology.

This ecotypic variation in drought resistance has some relation to root morphology and physiology. Kriebel (1963b) found that 4-year-old trees of the drought-resistant southern ecotype

subspecies *floridanum*) had a heavy primary root; it is rather short but quite thick and is accompanied by a dense mass of fine roots. Trees of the other two ecotypes had a diffuse root system without a thick central root. The absence of a tap root was offset in drought-resistant trees from western

regions by long, deeply penetrating roots (fig. 4). The top-root ratio of population samples appeared to vary inversely with latitude of origin, but seedling survival was mainly related to depth of root penetration, rather than to the ratio of tops to roots in terms of size or dry weight.

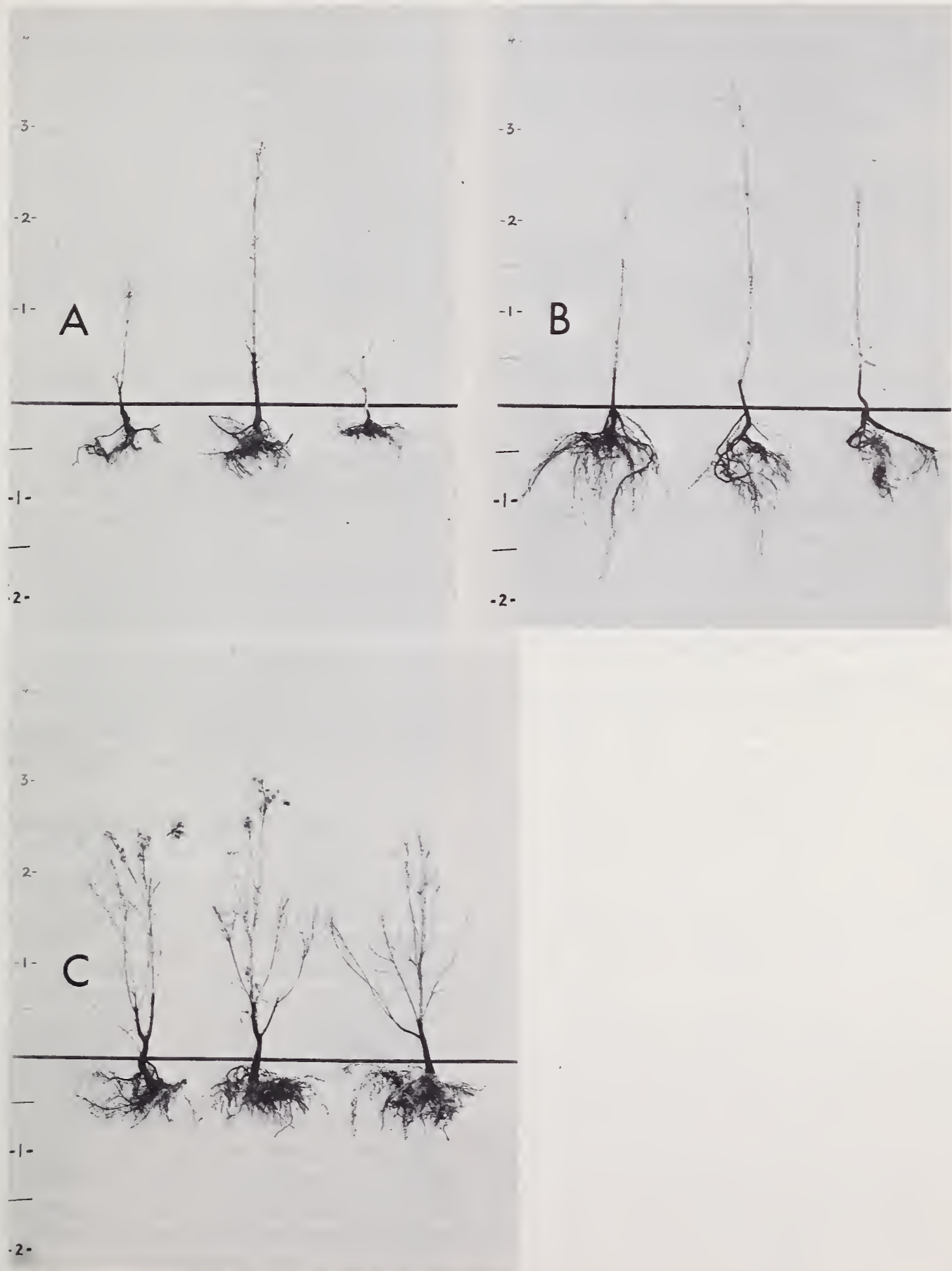


Figure 4.—Ecotypic variation in top and root structure of 4-year-old hard maples taken from an experimental nursery at Wooster, Ohio. Geographic origin: *A*, Vermont, *B*, central Illinois, and *C*, Georgia.

Variation in Chilling Requirements

Seeds of subspecies *floridanum* germinate in less than 90 days while still in stratification at 5° C. In contrast, seeds of northern genotypes require a longer period of stratification for germination. In subspecies *saccharum*, the chilling requirement seems to be greater in seeds of northern origins than in samples from farther south. In a comparison of samples from three Ontario origins, seeds of the southernmost origin germinated in stratification a month earlier than did seeds of the two northernmost sources. Seeds from central Ontario were next to germinate. Samples from northern Ontario were the last to attain a maximum germination rate. The consistency within sources and the south-to-north trend suggest that this differential response is at least partly the result of genetic selection (Kriebel 1958).

There is experimental evidence of geographic variation in chilling requirement for bud-break and stem elongation. Trees of Georgia, Tennessee, Ohio, and Michigan origin were moved into a warm greenhouse after successively longer periods of outdoor chilling in Ohio. Results demonstrated that variation in chilling requirement is latitudinal and that northern trees require more chilling for normal bud activation than southern trees. When the chilling period was only slightly longer than the absolute minimum for bud-break, flushing was restricted to lower buds. Additional, though sub-optimal, chilling resulted in normal flushing, but there was a long period of post-chilling dormancy, and flushing was a slow process. As the length of the chilling period was increased, the period prior to bud-break was shortened and leafing-out was hastened. The chilling requirement was fully met in Ohio by late January in southern trees and by mid-February in northern trees (Kriebel and Wang 1962). The variation pattern is probably continuous because of the gradual southward progression of the seasonal temperature transition.

Further proof of geographic variation in the chilling requirement for flushing and growth was obtained from a field test near Gainesville, Fla. Winter temperatures were sufficiently low to provide adequate chilling for bud-break of northern trees as well as Georgia trees, but the latter were the first to leaf-out. Trees of more northern origins leafed-out later, all at about the same time and at a slower rate than they did in Ohio. Apparently chilling of these northern trees, though sufficient for bud-break, was inadequate for maximum rate of growth initiation (Kriebel and Wang 1962).

Variation in Flushing Time

Geographic variation in time of growth initiation is clinal in field tests at northern latitudes. In provenance tests in Ohio, where winter chilling is adequate for all genotypes, northeastern trees begin growth first. The cline moves in a south-westerly direction with regard to seed source, then eastward through trees of central Appalachian origins. In mid-latitude population samples, development is most rapid among trees from the region just west of the Appalachians; Ohio valley trees leaf out ahead of trees from central Appalachian and Illinois sources. Flushing of *floridanum* trees occurs at nearly the same time as does flushing of trees of Illinois origin. Southern Wisconsin trees are also late in leafing-out, compared with trees from the same latitude farther east.

The well-defined geographic pattern has a significant relationship to the contemporary warm-season temperature pattern and to summer day length, but other factors are also involved. One would oversimplify by describing such a variation pattern on the basis of regression on climatic variables without considering effects of evolution. Such effects are suggested when the clinal pattern is plotted on a map of eastern North America by the use of isometric lines, which roughly parallel the shifting boundary of late glaciation. Also, trees from the region representing the Ozark-Ouachita glacial refugium leaf-out earlier than those from surrounding areas, especially trees from the Mississippi Valley to the east.

This variation pattern in flushing, and the high level of winter hardiness in southern genotypes, indicate that the geographical distribution of genes affecting these physiological characters strongly reflects the selective influence of earlier climatic conditions and consequent "migration" of genotypes (Kriebel 1957a, 1957b).

Juvenile estimates of the relative flushing time of trees of a particular geographic origin indicate later performance. The coefficient of correlation between 30 source means at ages 7 and 14 in an Ohio provenance test was +0.97, indicating a high level of repeatability. The correlation coefficients for comparisons of 2-year-old nursery trees with 7- and 14-year-old plantation trees, based on source means, were +0.84 and +0.80, respectively.

Variation in Time of Onset of Dormancy

The time of shoot growth cessation varies between provenances. Trees from northern sources are the first to stop growing; in Ohio shoot growth of northern trees stops in June. Trees from the Gulf Coastal Plain often continue to grow until killed back by frosts. The geographic pattern of variation is not well defined, and seems to be the result of a complex set of conditions, including decreasing temperature and day length (Olmsted 1951, Kriebel 1957b).

The time of fall leaf coloration, like the time of flushing, is subject to strong genetic control. Variation is clinal, beginning with the northern trees and ending with the southern trees. It is closely correlated with summer day length of the provenance. Summer temperature of the source modifies the trend, by slightly advancing the time of leaf coloration in trees from seed sources in the comparatively cool regions of the middle and southern Appalachian mountains.

Black maples (subspecies *nigrum*) precede sugar maples (subspecies *saccharum*) of the same origin in the onset of dormancy in provenance tests (Kriebel 1957b).

The correlation between the time of fall leaf coloration at age 2 and that at age 7 was estimated to be +0.81. The correlation was based on source means, and it is approximately equal to the correlation between flushing times at these two ages. More juvenile correlations are needed for evaluation of the efficiency of early selection for time of fall coloration.

Variation in Branch Habit

In a hardwood species such as *A. saccharum* Marsh., the relationship between rate of height growth and vigor is not as direct as it is in many coniferous species. Apical dominance varies greatly within the species. A tree may be very vigorous in terms of the total amount of shoot elongation or branch production, even though it is not very tall. Therefore, tree form greatly affects rate of growth in height or in volume of usable product.

The pronounced geographic difference in branch habit between subspecies *floridanum* and the two more northern subspecies (*saccharum* and *nigrum*) has already been discussed. *Floridanum* is more likely to develop lateral branches and to be without apical dominance. This tendency is accentuated at northern latitudes by winter dieback of branch terminals (Kriebel 1957b).

There is also individual variation in branch habit within subspecies *saccharum* and *nigrum*. Some trees have ascending branches with no dominant central leader. Others have few ascending branches, a strong central leader and stubby lateral branches (Harkness 1954). Some of these types have been included in the nomenclature as "forms" or "varieties" (Desmarais 1952, Slavin 1954, Mulligan 1958). Because of the great variability in natural stands and provenance collections, these types should not receive such formal status, except for convenience.

Variation in Growth Rate

Growth rate comparisons may be made among individuals, families, and seed-source samples. The relative size of each of these components of variance depends partly on sampling technique (Kriebel 1965).

There was no significant height difference attributable to seed source in analyses of large numbers of 2-year-old sugar maple seedlings from 30 sources widely distributed over the species range. Individuals varied as much as tenfold within sources (Kriebel 1957b).

In contrast, in an analysis of 1-year-old seedlings of three Canadian sources distributed to the northern limits of the range, differences related to seed source were highly significant, though differences among families within sources were nonsignificant. There was very little variation within families (Kriebel 1958).

Results of a 14th-year evaluation of height growth in a 30-origin field test in northern Ohio are summarized as follows:

1. Source samples with the greatest rate of height growth came from a region ranging from central and southern Illinois, across Indiana and Ohio to northwestern Pennsylvania, southwestern New York, and southern Ontario just north of Lake Erie.

2. Samples with a moderate growth rate came from a region including the lower peninsula of Michigan and the southern and northeastern parts of the range of *saccharum*, excluding Quebec.

3. Samples with the lowest growth rate originated in a region ranging from Iowa and northern Illinois through Wisconsin and across the northern limits of the species distribution to Quebec.

Southern and southwestern genotypes of subspecies *floridanum* and the Missouri-Arkansas complex are not included in these data. Height growth of these trees is not comparable with that of northern types because of *floridanum*'s diffuse

branch habit. Vigor is high, but not in terms of height growth.

In a provenance test in southeastern Ohio on an eroded old field site, growth and survival of trees of nearly all sources were very low. A notable exception was the southern Illinois source, the only one which did not have high mortality or severe injury caused by drought, the periodical cicada (*Magicalada* sp.), and defoliating insects (Kriebel 1963a). Trees from this source were also superior in Tennessee, in an 8-year test of collections from 12 origins (Zarger 1956).

Other Ohio experiments indicate that juvenile selection of sugar maple for height growth is not practical on the basis of half-sib family or provenance means. Seedling-sapling correlation coefficients averaged +0.64 for 14 Ontario half-sib families, when height growth of 11-year-old trees was compared with that of 1-, 2-, and 3-year-old trees. In early correlations of height growth of 30 provenance samples, the average coefficient was +0.69, when 9th- and 13th-year height was compared with 2d- and 6th-year height, respectively. There was no apparent increase in correlation with increase in age at which the first measurements were taken.

Preliminary estimates of narrow-sense heritability of tree height, based on nine 50-tree Ontario half-sib progenies at ages 2 and 3, were 0.30 and 0.28, respectively.

Variation in Sugar Concentration and Volume of Sap

Individual trees in forest stands and along roadsides vary in sugar concentration and sap volume. A ranking of a series of trees tends to be consistent over a period of years (Taylor 1956).

There is recent proof that this individual tree variation in sugar concentration is inherited. A controlled breeding experiment was started in Ohio in 1955 to study inheritance of sugar content in sugar maple. The progeny test includes 12 families. These families represent crosses of local trees that are high, intermediate and low in sugar content, and also open-pollinated progenies of some of the trees. Sugar tests made in 1964, 1965 and 1966 showed the existence of very highly significant differences among families. Analysis of the data by Namkoong and Kriebel indicated that

additive effects were an important component of variance. In this first estimate, narrow sense heritability was 0.60. The highest sugar percentage readings were obtained from the cross of the two best parent trees. Five trees in the progeny of these two parents had individual test readings higher than the maximum reading ever obtained from either parent; 7.4 percent was the maximum reading obtained. Male and female lines were variable, as were female lines in a half-sib progeny test of 12 families. In the latter experiment, no significant differences have been obtained between families.

Sugar concentration is positively correlated with volume yield of sap. In a 14-year study of 27 trees, the correlation between average percent sugar concentration and total sap volume was +0.71 (Marvin, Morselli, and Laing 1967). The correlation indicates a fairly close association between the two traits.

Early tests show no relationship between geographic origin and sap sugar concentration (Kriebel 1960), but further study will be required. There is no significant difference in sugar content between subspecies *saccharum* and subspecies *nigrum* (Kriebel 1955).

Cytology and Mutations

Sugar maple is a cytologically stable species. Although polyploidy occurs in some species of maple (Taylor 1920, Wright 1957), no polyploids of *A. saccharum* Marsh. have been reported. Sugar maple has a diploid chromosome number of 26, including subspecies *saccharum*, *nigrum*, and *floridanum* (Taylor 1920, Darlington and Wylie 1956, Kriebel 1957b). In subspecies *saccharum*, 26 chromosomes were counted in developing leaf buds of Massachusetts, Ohio, and Tennessee origin (Kriebel 1957b).

Compared with other maples, the species is relatively free of mutations. No extremely abnormal growth forms have been recognized. Albinism is not common, although Kriebel found albinos among germinants obtained from seed of subspecies *floridanum* collected in a Jackson County, Fla., stand. Gabriel (1962a) found chlorophyll deficiencies after self-pollination, in the forms of albino, yellow, and pink cotyledons. Occasional seedlings were noted with procumbent stems which later became upright.

IMPROVEMENT PROGRAMS

Breeding for Timber Production

Breeding for timber production should concentrate on high-value products, especially lumber and veneer. Because of its attractive grain and desirable physical properties, sugar maple will probably continue to be a premium wood for furniture and interior finish. It cannot compete with other hardwoods in the wood fiber or chipboard market, because of its comparatively slow growth.

Principal products of interest to geneticists are furniture, flooring, millwork, paneling, and veneer. Figured grains (curly, wavy, and birdseye) may continue to be in demand. Future use for handles, woodenware, novelties, sporting goods, and musical instruments will be too limited to warrant breeding programs.

The principal objective of breeding for wood production will be to obtain more rapid growth while preserving existing superiority over other maples with regard to wood properties.

Some birdseye maple trees have been propagated by grafting after felling, to preserve valuable genotypes and to study the effect of cloning on grain characteristics. The clones are being tested in Wisconsin and Ohio. Results may indicate the feasibility of selection or breeding for this character.

Selection standards for sugar maple timber trees have not been established. Desirable visible characteristics of the living tree include a high degree of apical dominance, a long and straight bole, a rapid rate of growth in height and volume, and no evidence of insect, disease, or weather injury.

Simultaneous intensive selection for more than one or two traits at a time is impractical (Wright 1962). Even single-trait selection is difficult in sugar maple; plantations are not available and natural stands are usually mixed in species composition and age. Also, growth rate, a trait of prime interest, is probably low in heritability.

Genetic improvement of natural stands by selective thinning is not practical. Unless there is a high selection differential, genetic gain will be negligible. But a high selection differential would necessitate leaving too few trees for natural regeneration (Wright 1962).

Because of the limited knowledge of heritabilities of vigor, form and other characteristics, high genetic gain will be unlikely in the early stages of a selection program. The first step will be to select trees from the most promising provenances for the test region, using available information on variation patterns. The first generation of progeny

testing will probably be most effective if combined with second-stage provenance tests, using open-pollinated seed lots from the best phenotypes in the best stands in each provenance. The collections will be taken from a limited part of the species distribution. It would be too expensive to simultaneously establish separate provenance and progeny tests, and the long reproductive cycle makes it impractical to wait for results of second-stage provenance tests before beginning progeny testing.

Establishment and maintenance of sugar maple plantations is not as much a problem of technique as one of cost. Progeny tests must be made on good agricultural land, and must be given intensive care, especially during the first decade. The high cost limits the size of such tests and necessitates careful selection of provenances and of stands within provenances. The authors do not know whether intensive mother tree selection within stands, as suggested by Pitcher and Dorn (1967), is worthwhile. Evidence indicates that there is less within-stand variation in sugar maple than in red oak (Kriebel 1965).

A second type of improvement program should be initiated as soon as feasible. This is a controlled breeding program in which crosses are made between trees of different geographic origins, especially widely separated origins. Unless ways are found to induce early flowering, most provenance crosses will be made in the older plantations in northern Ohio for the first 20 years. In the oldest Ohio plantation, five trees flowered for the first time in 1968. These trees were in an 18-origin plantation of wildling collections, and were about 22 years old when they first flowered. Four were of subspecies *floridanum*.

Although population samples in the Ohio plantations are mostly small, a very wide geographic array of samples is present, and evidence indicates that within-origin variation is much less than variation from one geographic origin to another. There are also some grafted biotypes of different origins available which have flowered and can be used for initial crossing experiments.

Breeding for Maple Syrup Production

Substantial progress has already been made in selection for maple syrup production. The objective is to increase the yield of maple syrup from sugar bushes by developing improved planting stock with higher sap sugar content and greater volume yield of sap. Fortunately, the positive cor-

relation between these two characters (Marvin, Morselli, and Laing 1967) greatly facilitates selection and breeding. Selection for syrup flavor has also been considered, but this would require an entirely new program based on the uncertain long-range economic value of flavor variation. Too much time and effort has already gone into the existing selection programs for efforts to be diverted or expanded. There are indications of substantial genetic gain from present programs.

Genetic selection programs now underway are based on sap sugar content. Standards established in the Northeast require that a tree exceed the sweetest of the four or five surrounding comparison trees by a minimum of 0.5 percent sap sugar and be at least 30 percent above the average of the standards. A tree must be tested at least three times the first year and twice the second year before final screening. Final selection depends on ability of the selected tree to consistently maintain its superior position relative to its standards (Gabriel 1964). Research by Kriebel in Ohio and by Morrow (1952) in New York suggests the desirability of 3 years of sap testing prior to final selection. Tests should be made during the early or middle part of the sap season because sugar percentage tends to be higher during this period. When readings are low, differences between trees are small, genetic variation is masked, and comparisons are difficult or impossible.

Selections may be made among either forest stands or roadside trees. Roadside trees with deep crowns are frequently 50 percent higher or more in sap sugar content than are forest trees (Stevenson and Bartoo 1940, Kriebel 1960). This must be considered in making selections. Diseased, injured, or decadent trees should be eliminated in the selection surveys because such trees tend to be unusually high in sugar content. Selection is accomplished by direct measurement of sap sugar content, usually with a hand refractometer. Observations can be made easily and rapidly by this method, except on very young trees. There is no advantage in attempting indirect selection using correlated characters.

Selection is made on an individual-tree basis because sap sugar content varies individually more than among stands or geographic origins. Therefore, breeding requires family selection in full-sib progeny tests. These progeny tests should be designed for seed production. Maximum genetic gain will be obtained by controlled crossing in the progeny test plantations, rather than by random natural crossing of superior progenies or individuals. To save 15 to 20 years, all selections should

be propagated vegetatively as well as sexually. Until rooting problems are solved, this must be done by grafting or budding. After 8 to 10 years, flowering can be expected on grafts and controlled pollinations can be made. This type of breeding program was started in Ohio in 1955. If flowering conditions are favorable, second-stage crossing will begin in 1969 on grafts of progeny-tested trees. A larger-scale grafting program was initiated in 1967 in Vermont, including many selections from the Northeastern United States.

Improvement of Shade Trees and Ornamentals

An important objective of a breeding program for development of improved shade trees will be to obtain faster growth. Few homeowners want to wait 2 decades or more for a shade tree to reach the desired size. A breeding program for improvement in growth rate would apply to shade tree improvement as well as timber production.

Breeding for ornamental purposes will be mainly directed toward a single objective. Some possible objectives are: A narrow crown; colorful fall foliage; compact form and small size at maturity; and resistance to insects, disease, air pollution, or drought injury.

The type of selection program will vary with the objective. Narrow-crown types will be selected primarily from Appalachian and northern origins, within which single-tree selection will be required. These trees can then be propagated by budding. This method is, in fact, now being practiced by commercial nurseries. Rooting of cuttings can replace budding after a practical, large-scale method of rooting sugar maple has been developed.

Autumn foliage color varies among trees, and individual-tree selection is necessary. Color is better in trees of northern or middle-latitude origin than in the late-turning trees of southern origin. Vegetative propagation will be required.

The Florida sugar maple (subspecies *floridanum*) offers excellent possibilities for selection of compact types of small size at maturity. Trees of central Georgia origin are more hardy in the Midwest than are those of the Gulf Coastal Plain. Vegetative propagation of selected individuals should be possible because of the potential commercial value of the trees.

Selections of sugar maple from southern Illinois and possibly southern Indiana, of the type intermediate between subspecies *saccharum* and *floridanum*, are extremely hardy at all times of year in the Central States. The chances of obtaining

drought-resistant selections from these genotypes are good. Mass selection and direct use of open-pollinated seed from these origins may be practical if a drought-resistant tree of intermediate size

and bushy crown is the objective. If a single stem type of moderate branchiness is required, individual selection and vegetative propagation will be necessary.

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